# Visual word recognition: insights from MEG, and implications for developmental dyslexia.

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## Introduction

The ability to fluently and, seemingly effortlessly, read words is one of few uniquely special human attributes, but one which has assumed inordinate significance because of the role that this activity has come to have in modern society. A disadvantage in reading ability not only has profound personal impact for the individuals concerned, but in terms of economic and social problems also has a wider negative influence on society at large. According to current government figures in the UK, some 22% of 11 year olds do not reach the minimum standard required in English national curriculum tests. Despite its importance, however, the scientific understanding of the neural basis of reading, and more particularly the visual aspect of visual word recognition, is relatively poorly understood. Thus far, a coherent overarching model, that spans the various conceptual levels, from behaviour through functional description to neuroanatomy, has proven extraordinarily challenging to elucidate. A fuller understanding of the computational processing and neurophysiological basis of how the reading system functions would therefore represent significant progress.

As with most complex behaviours, visual word recognition is thought to result from the dynamic interplay between the elements of a distributed cortical and sub-cortical network. To fully understand how visual word recognition is achieved therefore, and how it may fail in developmental dyslexia, we need to identify not only the necessary and sufficient complement of nodes that comprise this network – its functional anatomy - but we also need to understand how information flows through this network with time and indeed how the structure of the network itself may adapt in both the short and long term. In this chapter we take a historical approach to reviewing recent MEG (magnetoencephalography) research which elucidates these temporal dynamics, focusing particularly on events with the first 300ms of a visually presented word, and which we believe should set crucial constraints on models of visual word recognition and reading.

## Equivalent Current Dipole (ECD) Modeling:

In our first attempts to explore the temporal sequence of cortical activation for visually presented words, we used equivalent current dipole (ECD) modeling of MEG data. This technique is based on source modeling of evoked averaged data, and can therefore only reveal current sources in the brain that show a high degree of phase synchrony across trials. Unlike minimum current estimation (MCE) (Uutela, Hämäläinen and Somersalo, 1999) and minimum norm estimation (MNE) (Hämäläinen and Ilmoniemi, (1984), whose solutions give a spatially distributed estimation of current spread, multi-dipole ECD models render a set of tightly focused point sources for each subject for each experimental condition. At the individual level, this can give the impression that activity is well localised in the brain with ECDs. While this may be true for auditory and somaesthetic cortex, where very clear dipolar field patterns are reliably seen, this is rarely the situation for tasks which involve a widely distributed cortical network, such as reading and visual word recognition. As a result, we tend to see considerable variability in terms of anatomical localization across different subjects. Therefore, we suggest that the best way to interpret the data from multi-dipole models is in terms of robust, but rather simplified views of brain activation, in which the temporal sequence and response characteristics of a set of relatively coarsely defined ROIs can be described.

In a series of four studies of word reading and visual word recognition (Cornelissen, Tarkiainen, Helenius & Salmelin, 2003; Helenius, Tarkiainen, Cornelissen, Hansen & Salmelin, 1999; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Tarkiainen, Cornelissen, & Salmelin, 2002), we applied the following logic to stimulus design. As Fig. 1 A shows, we presented dark grey stimuli, such as letter strings, symbol strings, objects and faces on a light gray background. We then systematically varied the visibility of such stimuli by adding increasing amounts of pixel noise. This manipulation has two useful properties which allow us to look for dissociations in the patterns of evoked response. First, as noise increases, stimulus visibility reduces. This means that cortical areas which are sensitive to higher-order stimulus properties should show increasingly weaker responses as a function of increasing stimulus noise. Second, as pixel

noise increases so does the number of contrasty edges in the image. Therefore, any neurons which are primarily tuned to low level image properties, such as contrast borders, should show an increase in the amplitude of their responses as a function of stimulus noise. By using these manipulations we identified two main response patterns, and these are illustrated in Fig. 1 A & B.

[Figure 1 A & B about here]

The first of these, which we called Type I, took place around 100 ms after stimulus onset. It originated in the midline-occipital region the vicinity of V1/V2/V3 and was distributed along the ventral visual stream. This response was systematically and monotonically modulated by noise but was insensitive to the stimulus content, suggesting involvement in low-level analysis of visual features. The second pattern, which we call Type II, took place around 150 ms after stimulus onset and was concentrated in the inferior occipito-temporal region with left-hemisphere dominance. This activation was greater for letter-strings than for symbol-strings. The response to noise masking was nonlinear: response amplitude increased moderately with increasing pixel noise, and then as stimulus visibility became severely impaired at even higher noise levels, response amplitude reduced back towards baseline. We argue that this very different pattern of responses is therefore likely to reflect an object-level processing stage that acts as a gateway to higher processing areas. In addition, we also identified a third pattern of response (Type III). This also occurred in the time window around 150 ms after stimulus onset, but originated mainly in the right occipital area. Like Type II responses, it was modulated by string length, but showed no preference for letters as compared with symbols.

These data suggest an important role for the inferior occipito-temporal cortex in reading within 200 ms after stimulus onset and are consistent with findings from intracranial recordings (Nobre, Allison & McCarthy, 1994) and earlier MEG results (Salmelin, Service, Kiesilä, Uutela & Salonen, 1996). Nobre et al. (1994) demonstrated letter-string specific responses bilaterally in posterior fusiform gyrus about 200 ms after stimulus onset. MEG recordings by Salmelin et al. (1996) showed strong transient responses to

words and nonwords in the bilateral inferior occipito-temporal cortex in fluent readers at 150-200 ms. However, in dyslexic subjects, the left- but not right-hemisphere response was missing, suggesting a special role for the left inferior occipito-temporal cortex in fluent reading within the first 200 ms after seeing a letter-string (Helenius, Tarkiainen, Cornelissen, Hansen & Salmelin, 1999).

The fact that the Type II occipito-temporal response at ~150ms is stronger for letter- than symbol-strings in a silent reading task suggests a degree of orthographic selectivity. This raises the question whether it may also be sensitive to the lexical status of the letter-string. However, other data suggests that the Type II response is prelexical. The strength of this response as well as its latency, are very similar for words, nonwords and consonant strings (Cornelissen, Tarkiainen, Helenius, & Salmelin, 2003; Salmelin et al., 1996). Moreover, in these studies the effect of lexicality (i.e. words > nonwords or words > consonant strings) only starts to appear at about 200 to 300 msec after stimulus onset (see Fig. 2), in perisylvian cortex including the left superior temporal and inferior parietal areas (Marinkovic et al., 2003; Cornelissen et al., 2003; Helenius, Salmelin, Service, & Connolly, 1998) and at the base of the left anterior temporal lobe (Nobre et al., 1994).

[Figure 2 about here]

## Source Reconstruction With Synthetic Aperture Magnetometry (SAM):

Synthetic aperture magnetometry (SAM) is an adaptive beamforming technique for the analysis of EEG and MEG data (Robinson & Vrba, 1999; Van Veen et al., 1997; Vrba & Robinson, 2001). It is a second-order technique for solving the inverse problem and uses a linear weighting of the sensor channels to focus the array on a given target location or set of locations – in this case a regular array of virtual electrodes (or voxels) in the brain placed 5mm apart from each other. The result is a reconstruction of the time series for every voxel or virtual electrode in the brain. Thereafter, for a nominated frequency range,

it is possible to compare the power in the Fourier domain between a passive or baseline time window and a sequence of active time windows of interest, as well as to compute time-frequency plots for particular virtual electrodes of interest. As a result, it is possible to image changes in spectral power for both event related synchronization (ERS) (i.e. where power in the active window > passive window) and event related desynchronization (ERD) (i.e. where power in the active window < passive window).

The main advantages of source reconstruction techniques like SAM are twofold. First, unlike ECDs, it is possible to localize sources in the brain with SAM based on both evoked and induced activity, be they ERSs or ERDs. Epochs of evoked activity are those which are tightly phase-locked to the stimulus across successive trials, whereas induced activity is not (see Hillibrand & Barnes, 2005). In the amplitude domain, simple averaging across trials is sufficient to reveal an evoked signal component which will also be reflected in the frequency domain. In comparison, simple averaging in the amplitude domain will not reveal sources of induced activity because of phase jitter from one trial to the next, but such sources will still be revealed in the frequency domain. The second advantage is that using the appropriate anatomical information from an individual enables individual SAM statistical maps to be transformed to a standard MNI space and used to make group statistical inferences. The main limitation of adaptive beamformer techniques is dealing with sources that are perfectly temporally correlated. However, perfect neural synchrony between two sources in the brain over the entire course of the experiment is exceedingly unlikely, and it has been shown that two sources can be resolved even at relatively large temporal correlation levels (Sekihara et al., 2002; Van Veen et al., 1997).

## Lexical decision

We recently used SAM analysis of MEG data from a visual lexical decision task to map the spatiotemporal evolution of cortical events during visual word recognition (Pammer et al., 2004). As Fig. 3 shows, during the first ~150 ms following the central presentation of 5-letter words, we saw event related synchronization (ERS) in primary visual areas in the lingual gyrus, cuneus (BA17).

[Figure 3 about here]

In the same time frame, we also saw bilateral ERS in the inferior and middle occipital gyri (BA 18/19) with the responses being stronger in the left (LH) than the right hemisphere (RH). These findings are entirely consistent with other MEG studies of visual word recognition and reading using equivalent current dipole modeling (Tarkiainen et al., 1999; Salmelin et al., 2000; Cornelissen et al., 2003), minimum norm current estimation (Dhond et al., 2001) and dynamic imaging of coherent sources (DICS) (Kujala et al., 2007). After ~150ms, we saw event related desynchronization (ERD) in the left and right fusiform gyri (LH > RH) which expanded systematically in both the posterior–anterior and medial–lateral directions over the course of the next 500 ms. In the LH, that part of the mid-fusiform region which has recently been dubbed the visual word form area (VWFA) was activated around ~200 ms post-stimulus; this is in good agreement with the timing of word-specific responses from other neurophysiological recordings (Cohen et al., 2000; Nobre et al., 1994).

## Comparing SAM with ECDs and fMRI

On the basis of anatomical location and timing, there appears to be good correspondence between the ERS in lingual gyrus and cuneus identified with SAM and the Type I sources defined with equivalent current dipole modeling. Similarly, the ERS in the left and right MOG defined by SAM would appear to correspond reasonably with the Type II ECD response. Nevertheless, despite the fact that both sets of results are based on MEG data recorded during visual word recognition tasks, the SAM maps in Fig. 3 show a much finer anatomical parcellation of functional activation than is the case with ECDs. For example, the SAM maps show activations in the MOG which are distinctly separate from those in the fusiform gyri, whereas the published ECD results have never convincingly separated two such components. One explanation for this difference could be that the activation in MOG is largely phase-locked, whereas that in the fusiform is not. If so, ECD algorithms would likely fail to ‘see’ the fusiform activation. Alternatively, it may be the

case that fixed location, fixed orientation dipoles (as were used in Tarkiainen et al., 1999) are not sensitive enough to separate out two sources which are both close to each other and active within a similar timeframe. Fortunately, the application of a third analysis technique to these kinds of MEG data, minimum norm estimation (see Marincovic et al., 2003), does help us to resolve this apparent discrepancy because it also suggests that there is a systematic spread of activation along the ventral stream, from V1 towards the lateral occipital complex and the fusiform gyrus, during visual word recognition.

[Figure 4 about here]

The comparison between fMRI and SAM data throws up another striking difference between the results from different imaging modalities. As Fig. 4 shows, based on the meta-analysis of fMRI studies of reading by Vigneau et al. (2005), the appropriate fMRI contrasts for visually presented words tend to reveal a spatially restricted response in the mid-fusiform gyrus [average Talairach coordinates: x = -43, y = -54, z = 12], even though this can extend as far as ~ 4cm antero-posteriorly (see for example Vinckier et al., 2007). Among many others, Cohen et al. (2000) showed that the this so-called visual word form area (VWFA) responds more strongly to alphabetic letter strings than to checkerboard stimuli, more strongly to words than to consonant strings, and demonstrates invariance with respect to retinal position. In addition, VWFA shows font-type invariance (Dehaene et al., 2002). At issue here is not the validity of the interpretation as far as the role of this neuronal population is concerned. Instead, it is the very different impressions of what might be going on, depending on whether information about timing (in the millisecond range) is available or not. On the one hand, the fMRI data tend to produce a single, static blob of activation in the left mid-fusiform or VWFA because information is integrated over a long (~500ms) window. This therefore gives the strong impression that a relatively fixed population of neurons is doing something that contributes en masse to letter-string processing – whatever that is. On the other hand, it is very tempting to interpret the SAM and minimum norm estimates as evidence of a progressive sweep of cortico-cortical activation along the fusiform gyrus, that evolves with time. This more dynamic pattern is consistent with recent computational and conceptual models of visual word recognition

(see for example, Whitney, 2001; Dehaene, Cohen, Sigman & Vinckier, 2005), which suggest the idea of a time dependent sequence along the fusiform in which progressively complex attributes of letter-strings are extracted: from simple lines and edges in a retinotopic spatial framework, through to font and case invariant letters, letter-clusters, and ultimately whole words. For example, the LCD model proposed by Dehaene et al. (2005) suggests a succession of larger and larger receptive fields, from V1, though V2, V4 and V8 to OTS which extract letter fragments, then case-specific letter shapes, then abstract letter identities, then letter-clusters and so on. Therefore, in skilled readers in whom the visual word recognition network has been trained over hundreds of thousands of hours on central presentations of words, we ought to expect stimulus driven, bottom-up responses which reflect this tuning (see e.g. Nazir et al., 2004; Polk & Farah, 1998).

## Retinotopicity and hemifield presentations

In languages where the orthography is read from left to right, we tend to fixate on letters situated somewhere between the beginning and the middle of a word. According to recent research (Lavidor & Walsh, 2004; Lavidor, Ellis, Shillcock, & Bland, 2001; Monaghan, Shillcock & McDonald, 2004), this means that the letters falling to the left of fixation project initially *only* to the visual cortex in the right cerebral hemisphere while letters to the right of fixation project initially *only* to the visual cortex in the left cerebral hemisphere. There appears to be *no* overlap between the two. Consistent with this split fovea model, Cohen et al. (2000) recorded fMRI activations during the presentation of words, consonant strings and checker boards to the left and right halves of the visual field. As expected, they found position-invariant activation in the VWFA, especially for words. However, this activation was distinct from more posterior hemifield-dependent middle occipital gyrus (BA19) responses. These were stronger for contralateral than for ipsilateral stimulation, irrespective of whether the participants viewed words, consonant strings, or checker boards. Therefore, these data are consistent with retinotopic coding at this location in the reading network. Ultimately however, to confirm retinotopicity, it would be necessary to view these posterior activations in individual participants where not only have the boundaries between visual areas been carefully demarcated by

retinotopic mapping (see for example, Dougherty, Koch, Brewer, Fischer, Modersitzki, and Wandell, 2003), but also the word stimuli have been systematically shifted across the visual field relative to a fixation point.

[Figure 5 about here]

Fig. 5 shows results from our own MEG data in which 5-letter words were presented to the left and right upper and lower quadrants of the visual field. In these analyses, the data are averaged across the upper and lower quadrants, in order to compare the left and right hemisphere responses with each other. They show that within the first 250msec after stimulus presentation, the response to words in the region of the middle occipital gyrus is largely contralateral, suggesting processing within a retinotopic spatial framework. However, by around 300msec, the responses have become lateralized to the left fusiform. Thus, the left and right halves of words appear initially to be processed independently, in retinotopic cortical representations in the right and left occipital cortex, respectively. Some 50-100msec later, processing appears to localize, and to lateralize to the left hemisphere's (non-retinotopic) mid-fusiform cortex.

## Early Broca's activation

Surprisingly, Pammer et al. (2004) found an ERD in the left pars opercularis of the inferior frontal gyrus (IFG) and the precentral gyrus (BA44/6) which started early, at around ~100-200ms post-stimulus. This early IFG activity followed immediately after the bilateral ERS in middle occipital gyrus, and overlapped in time with the onset of activation in the LH mid-fusiform. Together, these findings suggest that the interplay between the vision and language domains starts early during visual word recognition.

The early involvement of Broca's area in visual word recognition may at first seem puzzling but in fact a number of other studies have also found indications of this. For example, in their analysis of evoked responses in a reading task, measured with MEG, Salmelin et al. (2000) report an early left frontoparietal activation (between 100-200ms

post-stimulus) in 5/10 stutterers and 5/10 controls. Kober et al. (2001) used MEG to identify responses in Broca's and Wernicke's areas in patients who carried out a silent reading task. While Kober et al.'s (2001) report focuses attention on the response in Broca's area at 720ms post-stimulus, nevertheless an earlier peak is clear in their data at around 170ms post-stimulus. Finally, Lachaux et al. (2008) measured cortical activity from surface electrodes implanted in epilepsy patients. Subjects were presented two inter-leaved stories in a rapid serial visual presentation (RSVP) format. Words from the story to be attended to appeared in one colour, while words from the story to be ignored appeared in a different colour. Time-frequency analysis based on data averaged in relation to word onset showed clear, early beta frequency band activity for both story-lines.

The required connectivity between extra-striate visual areas and posterior superior IFG could be supplied via the arcuate fasciculus. Recent DTI and histological studies of the arcuate fasciculus in human brains (Makris et al., 2005; Burgel et al., 2006) support Dejerine's (1895) original proposals, and suggest direct connections between Brodmann's areas 18 and 19 and the lateral frontal association areas. Moreover, DiVirgilio and Clarke, (1997) used the Nauta technique to demonstrate anterograde axonal degeneration in a post-mortem brain that had suffered a right inferior temporal infarction. These authors found crossed monosynaptic connections between extrastriate visual cortex and Wernicke and Broca's areas. In the current study we found a difference in latency between MOG (i.e. BA18/19) and IFG of around 10-15ms. Therefore, assuming no additional synaptic delays, this latency difference is consistent with the conduction velocity of a myelinated fibre of about 1 μ diameter over an 8-10cm distance (Patton, 1982). In summary, there is good reason to suppose that early activation in IFG to visually presented words is both plausible as an empirical phenomenon, and supportable by the known anatomical connectivity. Consistent with this, a Granger causality analysis reported in a recent MEG study of continuous reading (Kujala et al., 2007) also suggests that there are direct functional connections between occipitotemporal cortex and left hemisphere frontal areas during reading.

[Figure 6 about here]

The role of IFG in visual word recognition is well established from a number of neuroimaging studies (Bookheimer, 2002). The cortical regions in and around Broca's area in the inferior frontal gyrus (IFG) appear to be associated with fine-grained, speech-gestural, phonological recoding; direct stimulation / recording studies have shown very fast connections between this region in IFG and motor neurons in the motor strip which drive the speech articulators (Greenlee et al., 2004). This system has been found to function in silent reading and naming (Fiez & Petersen, 1998; Pugh et al., 1996; Pugh et al., 1997) and is thought to be more strongly engaged by low frequency words and pseudowords than by high frequency words (Fiebach et al., 2002; Fiez & Petersen, 1998 ; Pugh et al., 1996; Pugh et al., 1997). Moreover, functional connectivity between left dorsal IFG and occipito-temporal cortex for words, pseudowords, and letter-strings, but not false-fonts, has been demonstrated (Bokde et al., 2001; Mechelli et al., 2005). Haemodynamic functional imaging has therefore delimited quite precisely the anatomical extent of left posterior IFG activation during visual word recognition, and elucidated a likely role for it in phonological encoding.

However, while the functional connectivity data imply direct interplay between the vision and language domains, they cannot inform us about the time-course of these effects nor how they evolve over time. In contrast, neurophysiological studies using event-related potentials (ERPs) or fields (ERFs) can pinpoint events in time with millisecond precision, but they often face the converse problem that they lack anatomical precision. Nevertheless, a number of such studies have been carried out which indicate that interactions between visual and linguistic factors during visual word recognition do begin early. For example, Assadollahi and Pulvermüller (2003) showed an interaction between word length and frequency in MEG, with short words exhibiting a frequency effect around 150 ms but long words at around 240 ms. Effects of lexicality (i.e. a differential response between words and pseudowords) have been reported as early as 110 ms (Sereno et al., 1998), though more commonly around 200 ms (Cornelissen et al, 2003; Martin-Loeches et al., 1999). Lexico-semantic variables have been found to influence

brain responses as early as 160 ms after visual word onset (Pulvermüller et al., 1995; Pulvermüller et al., 2001), as has semantic coherence, which is a "measure that quantifies the degree to which words sharing a root morpheme, (e.g., gold, golden, goldsmith) are related to each other in meaning" (Hauk et al., 2006, page 1386). Intriguingly, Figs. 5 & 7 in Hauk et al. (2006) suggest early left frontal involvement particularly for semantic coherence, but unfortunately it is not possible to be more anatomically precise from their data.

## Virtual electrode analysis of responses in Broca's area, VWFA and MOG

Recently, we sought further evidence for early activation of IFG – specifically in the pars opercularis and precentral gyrus – in response to visually presented words. Based on our previous work and the studies reviewed above, we hypothesized that IFG activation should first be detected in a time window between the start of bilateral activation of the middle occipital gyri (MOG, BA 18/19) and the start of activation of the LH mid-fusiform (BA 37). Therefore, we used SAM analysis to identify six ROIs: one in each of the left and right MOG, the VWFA in left mid-fusiform and its right hemisphere homologue, and the left posterior IFG and its right hemisphere homologue. We tested the specificity of any early IFG activation by comparing responses to centrally presented words, consonant strings and faces. In addition, we wanted to ensure that the cognitive and attentional demands of the experimental task were held constant across different stimulus types by asking subjects to fixate on a central cross continuously, and to simply monitor and respond to any colour change of the cross. For each site and for each subject, we then calculated the timecourse of the MEG signal in order to compare the relative timings and amplitudes of responses to words, faces and consonants.

## Amplitude domain analysis: ERFs in Broca's area, VWFA and MOG

To examine the relative timings of evoked activity in these six ROIs, and also to compare responses to words, faces and consonant strings, we carried out further analyses in the amplitude domain, restricted to the time window 0-300ms post-stimulus. Significant differences between conditions in the resultant difference waveforms were computed using a nonparametric randomization technique, the Record Orthogonality Test by Permutations (ROT-p) (Achim, 1988 & 1995).

[Figure 7 about here]

Fig. 7(a) and (b) show the normalized ERFs for centrally presented words in the left IFG ROI, compared with its right hemisphere homologue, as well as word responses in the VWFA ROI compared to its right hemisphere homologue. Consistent with our hypothesis, the left IFG showed a significantly stronger, early response at ~125ms to words than its RH homologue. As would be expected on the basis of haemodyamic neuroimaging studies, we also found a significantly stronger response to words in the VWFA at ~150ms than its RH homologue.

[Figure 8 about here]

Fig. 8 shows pair wise comparisons between words and faces (Fig. 8a) and words and consonant-strings (Fig. 8b) for all six ROIs. ROT-p analyses showed significantly stronger responses to words than to faces in left and right MOG, left IFG, and VWFA, between ~80 – 150ms post-stimulus. We also found a significantly stronger response to faces than to words in right IFG between ~150-200ms. Moreover, Fig. 8a shows that the peak response to words in the left IFG ROI occurred ~10-15ms later than the commensurate peaks in left and right MOG but ~20ms earlier than that in VWFA. Formal satistical comparisons showed the former difference, but not the latter, to be significant at $p<0.05$.

## Frequency domain analysis: Spectrograms in Broca's area and VWFA

Since the amplitude domain analysis failed to show a significant difference between the evoked responses to words and consonants in the left IFG and left mid-fusiform, we also carried out the complementary analysis for these ROIs in the frequency domain. To examine the time-course of any changes in oscillatory activity within each ROI, time-frequency plots (or spectrograms) were calculated using a Morlet wavelet transform. Time-frequency plots contain information about both the evoked and the induced components of the neuronal response (Hillebrand et al., 2005a & 2005b). Fig. 9 illustrates the results. Each plot represents the grand average of the differences between each participant's word and consonant spectrograms.

[Fig. 9 about here]

Fig. 9 shows the left IFG responses to words were stronger than those to consonants (red) in both the alpha and beta frequency bands first around ~130ms post-stimulus and also later at ~400ms post-stimulus. In the left mid-fusiform (VWFA), Fig. 9 shows a stronger response to words than consonants at ~300ms post-stimulus. The dotted black lines in Fig. 9 represent regions in the time-frequency plots where mixed modeling showed significantly more power for words than consonants at $p<0.05$, controlling for any effects of spatial time-frequency covariation.

## Response specificity: MOG and VWFA

The amplitude domain analyses showed stronger responses to words than faces in left and right MOG, where retinotopicity is maintained. Our experimental task arguably minimised differences in attentional demands and cognitive loading between stimulus classes because participants only had to monitor and respond to colour changes in the fixation cross. Therefore, this leaves two main reasons in principle for stronger responses to words than faces. Consistent with the electrophysiological findings reviewed earlier (e.g. Cornelissen et al., 2003; Tarkiainen et al., 1999; Hauk et al. 2006; Pulvermuller et al. 1995; Pulvermuller et al. 2001; Sereno et al. 1998), one possibility is that these differences may genuinely reflect word specific effects related to early interactions

between the vision and language domains. However, there is a second possibility. The MOG ROIs were located in retinotopic extra-striate visual cortex (see e.g. Dougherty et al., 2003; Brewer et al., 2005). Therefore, since the horizontal extent of the words on the retina exceeded that of the faces, it is quite possible that the stronger response to words merely reflected activity in more peripheral receptive fields. The word/consonant string comparisons allow us to disambiguate these possibilities for MOG, because, unlike faces, word and consonant strings were the same size. For left MOG Fig. 8 showed that evoked word responses were stronger than consonant-string responses around 100ms post-stimulus. This differential response for stimuli with the same retinal subtens is therefore more consistent with word specific than low level visual effects (where we would have expected no differences between words and consonant strings). However, for right MOG, the picture is less clear because, responses to consonant-strings were no different from those to words.

At the VWFA site, we found an evoked response to words that peaked around 150ms post-stimulus, was stronger at this time point for words than faces, but was not distinguishable from the commensurate evoked response to consonant strings. However, the frequency domain analyses for words demonstrated both ERD and ERS in the alpha and beta frequency bands respectively from ~ 120ms post-stimulus onwards. Critically, the direct comparison between words and consonants revealed a significantly stronger response to words in the beta band between ~250-450ms post-stimulus. These results are consistent with haemodynamic neuroimaging studies which suggest word specific responses in the left mid-fusiform (e.g. Cohen et al., 2000; Dehaene et al., 2002; Ben-Sachar et al., 2006).

Put together, the results for left MOG and left mid-fusiform are consistent with recent models for letter-strings encoding along the occipito-temporal complex, which assume that there is a hierarchy of information processing on a continuum from simple features through to increasingly elaborate and abstracted objects as discussed above.

## Response specificity: IFG

Left IFG gave a stronger evoked response at ~125ms to words than the right IFG. Moreover, the evoked response in left IFG at this time was stronger to words than to faces. In the frequency domain, we found a significantly stronger response to words than consonants in both the alpha and beta bands both at around ~125ms post-stimulus as well as later at ~400ms post-stimulus.

The simplest way to interpret this pattern of results is to assume that the same stereotypical response to any equivalent length string of letter-like objects would always be produced, irrespective of task demands i.e. whether explicit naming is required or whether stimuli are viewed passively as in the current experiment. If so, this might suggest that for a skilled reader who has had many thousands of hours of experience with print, the very presence of word-like stimuli in the visual field can trigger a response in IFG, and its role is to prime the rest of the language system to prepare for upcoming crossmodal interactions between the vision and language systems - a stimulus driven anticipatory response. It is also possible that such an effect, if true, may have been further enhanced by the blocked design of the current study. This proposal is similar to recent claims by Bar et al. (2006), who showed that low spatial frequencies can facilitate visual object recognition by initiating top-down processes projected from orbitofrontal to visual cortex; object recognition elicited differential activity that developed in the left orbitofrontal cortex 50 ms earlier than it did in recognition-related areas in the temporal cortex.

An alternative possibility is that early IFG activation in response to visually presented words reflects grapheme-to-phoneme conversion processes, perhaps along the sublexical route for reading (Coltheart et al., 1993; Harm and Seidenberg, 2004). This interpretation is in line with other imaging studies that have implicated this frontal area in phonological processing during visual word recognition (Burton et al., 2005; Joubert et al., 2004), and with priming studies showing early activation of phonological representations (Carreiras et al., 2005; Lee et al., 1999; Lukatela et al., 1998; Lukatela and Turvey, 1994). Moreover, this possibility is in alignment with research on verbal short term memory.

Effects of word length and phonological similarity indicate that visually presented items, such as letters or numerals, are recoded into phonological form prior to storage in short term memory (Baddeley, 1986; Conrad and Hull, 1964). Articulatory suppression removes the phonological similarity effect, indicating the importance of articulatory processes for such recoding (Baddeley, 1986). Indeed, one fMRI study specifically showed activation of IFG, inferior parietal cortex, and posterior temporal cortex in response to working memory for letters versus abstract symbols (Henson et al., 2000). Imaging studies have also indicated that inferior parietal cortex encodes the phonological information itself, providing the so-called phonological store (Baddeley, 1986) while IFG also controls the rehearsal process via reactivation of information within the phonological store (Awh et al., 1996; Henson et al., 2000; Paulesu et al., 1993). Thus, it appears that visual information is recoded into an articulatory-phonological form in IFG, which activates an auditory-phonological representation in inferior parietal cortex, which in turn activates lexical forms in temporal cortex (Henson et al., 2000).

## Implications for developmental dyslexia

The overriding impression from the MEG studies of visual word recognition reviewed here is that the functional connections between the nodes of the reading network seem to ignite multiple and/or parallel routes very quickly after words are presented. This runs counter to the idea of an orderly sequence from visual processing of letter strings, to grapheme-phoneme mapping, to semantic mapping to spoken output. Moreover the MEG data from the reading and visual word recognition studies of dyslexic individuals, reported by Salmelin et al. (1996) and Helenius et al. (1999) are very compelling. They suggest that the first detectable differences between the reading networks in dyslexic and non-dyslexic readers emerge very early and are located essentially in extra-striate visual cortex. While the designs of these studies do not allow us to identify the causes of these differences, there is a range of possible explanations consistent with the data that lie between two extreme positions. At one extreme, these differences could in principle derive from a low-level deficit in visual processing of letter-strings. This represents a strictly bottom-up account of the problem, placing the primary impairment squarely in

the visual domain. At the opposite extreme, we can imagine either top-down, or feedback-feedforward influences at work over the months and years that children learn to read. For example, it is possible that either a failure of network integration, or a primary deficit higher up in the network – such as a tatty phonological representation - could result in differences in the way that the reading network crystallizes out over time. In this view, there is nothing particularly special about the lack of a left hemisphere occipito-temporal node in the dyslexic brain. It is merely one of a cluster of differences between the normal and dyslexic reading network, and is notable only for being the first to emerge in the temporal sequence of events in cortex during visual word recognition.

Intriguingly, the data from Rosen (this volume) suggest that developmental dyslexia is indeed associated with genetically determined differences in anatomical network integrity. If true, this may well impact on: a) the spatio-temporal precision of information flow between the nodes of a distributed network, such as that for reading, and b) the precision with which information may be transformed at the synapses contained within the nodes of the distributed network. If the integrity of thalamo-cortical and cortico-cortical loops is compromised, we might also predict that MEG could identify differences of 'at rest' measures of oscillatory activity in the brains of dyslexics. Moreover, while there is still debate about the prevalence and the impact of low-level visual processing differences in developmental dyslexia, the elegant findings from Ramus (this volume) suggest that there may not be an isolable deficit with phonological representations in developmental dyslexia. In our own work measuring perceptual confusions between spoken CV syllables in noise (Cornelissen et al., 1996), we also struggled to find any convincing evidence for systematic differences between the input phonological representations of non-dyslexic and dyslexic adult readers.

Given these challenges to the phonological deficit theory of dyslexia, let us go out on a limb here and suppose that dyslexics do *not* have visual processing deficits and do *not* suffer distorted phonological representations. How then could we explain impaired visual word recognition? Before we go further, I want to acknowledge that a long history of experimental research in psychology has taught us to be extremely cautious about

developing arguments and theories based on personal experience and anecdote. Nevertheless, particularly in the clinical world, it is frequently the anecdotal story – the patient with the odd symptoms who doesn't seem to fit recognized pattern – that leads to new insights. So, with these caveats in mind, I offer the following observation as an inspiration for how we might conceive of impaired reading without visual / phonological representational deficits.

At Chirk Castle in Wrexham, North Wales, UK, there is displayed on one wall of the museum a written proclamation dating from the time of Charles I. The manuscript is written in a flowing, highly decorative calligraphy in unfamiliar Old English which is peppered with unfamiliar spellings. What surprised me on a visit there once was the complete inability of a highly literate English speaking colleague of mine to read this manuscript. Though normally completely fluent in reading, this manuscript completely stumped him. There was no doubt he could slowly make out individual letters and work out individual sounds. But with this manuscript, what he could not do was to string the letters and sounds together quickly enough into working memory to obtain any sense of fluency. It was as if the extra burden the unfamiliar script imposed on his decoding skills pushed him to a tipping point and precipitated a catastrophic collapse. As a result, any possibility of his extracting meaning and context from the text completely evaporated.

What, if anything, can we draw from this anecdote? The first point to make, especially given the claims for impaired working memory in dyslexia, is the importance of integrating enough information into a large enough memory buffer quick enough to obtain fluency in reading. The second point to this story is that the noise introduced into my colleague's reading system was at a minimum caused by the slow extraction of orthographic features. But it is not hard to see how the bottleneck(s) could be placed a little further into the system, so that there is no longer a problem with feature extraction per se, nor a lack of fidelity of representation, but slowed transmission and integration of information within and between network nodes. Arguably, and now I really want to go out on a limb here, reading is also one of the very few cognitive task where deficits in network integrity might be *expected* to cause the greatest devastation.

From a purely visual perspective, printed words represent a very unusual visual stimulus and are quite unlike images from the natural world (Cornelissen and Hansen, 1998). Specifically, all the information available in a line of text is compressed into three discrete spatial scales, to a first approximation: coarse, intermediate and fine. Roughly speaking these scales correspond to: the average size of a word, the average size of a letter and the average thickness of the lines that makes up each letter. There is no other useful information at intermediate spatial scales. This contrasts dramatically with natural images which contain a smooth continuum of information across all spatial scales (Tolhurst et al., 1992). Over and above their visual peculiarities, printed words are also unusual in the sense that the cognitive targets of familiar words are pre-existing semantic concepts which can only be reached via a complex set of learnt transforms involving the vision and the language systems. When we read for meaning, the sensory inputs for visual word recognition are not the direct sensory correlates of the semantic targets themselves, as is the case with seen objects, heard sounds or felt objects. Instead, the situation with reading is much more indirect; printed words are visual symbolic representation of the speech/sound codes for the *verbal labels* for the semantic targets. This suggests to me at least that reading may make an anomalously high demand on an individual's capacity to integrate information across different domains – so that network integrity becomes absolutely key to success in reading. Commensurately, failure of network integrity may in and of itself be sufficient to explain reading failure.

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***Fig. 1A Type I ECDs and mean amplitude of response to 1- and 4- element symbol and letter strings.***

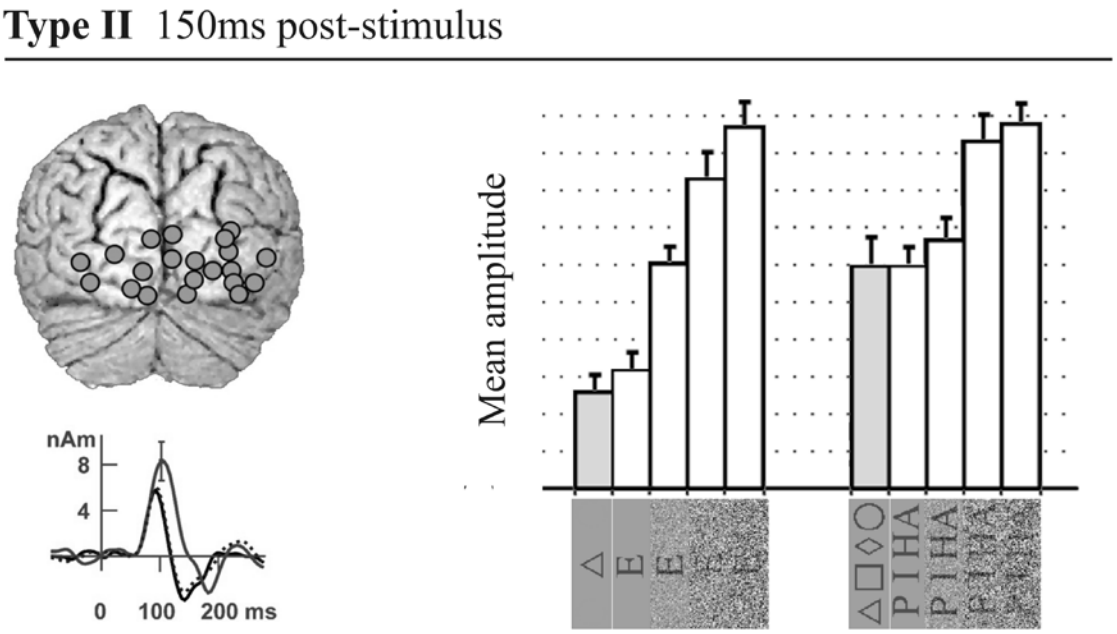


***Fig. 1B Type II ECDs and mean amplitude of response to 1- and 4- element symbol and letter strings.***

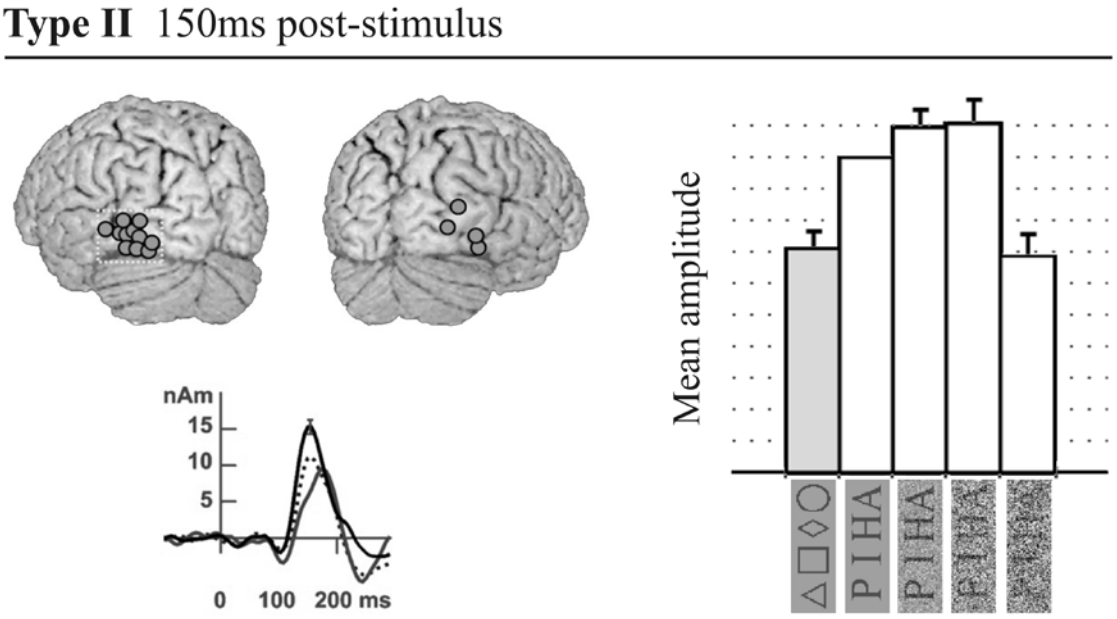

***Fig. 2 Type I & II ECDs together with ECDs showing significantly stronger responses to 6-letter Finnish words than 6-letter consonant strings. Plot showing grand average waveforms for each of the three ECD types, separately for words and consonant strings.***

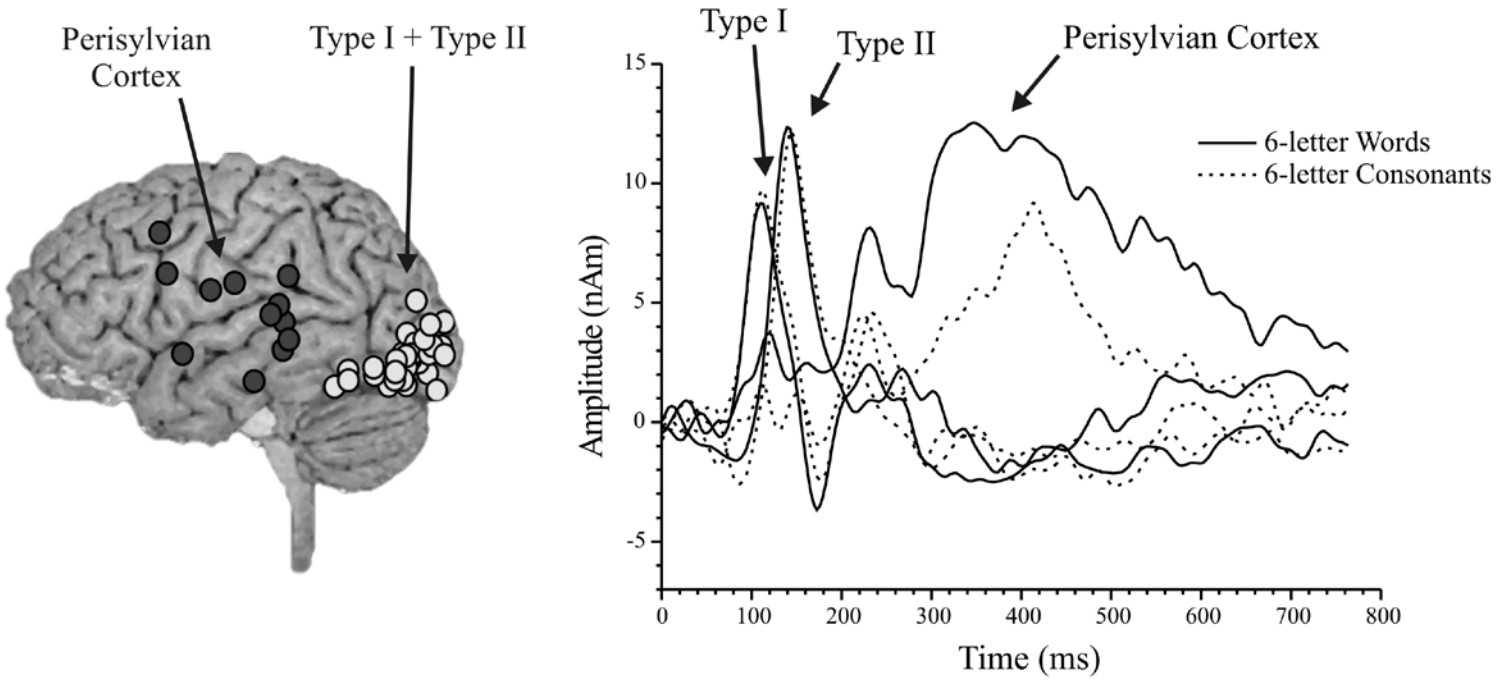

***Fig. 3 Group SAM maps of responses in the beta frequency band (10-20Hz) to 5-letter words. MOG = Middle Occipital Gyrus; MID FUS = Mid Fusiform Gyrus (VWFA); IFG = Inferior Frontal Gyrus. ERS and ERD thresholded at p<0.05 are shown in white and black respectively.***

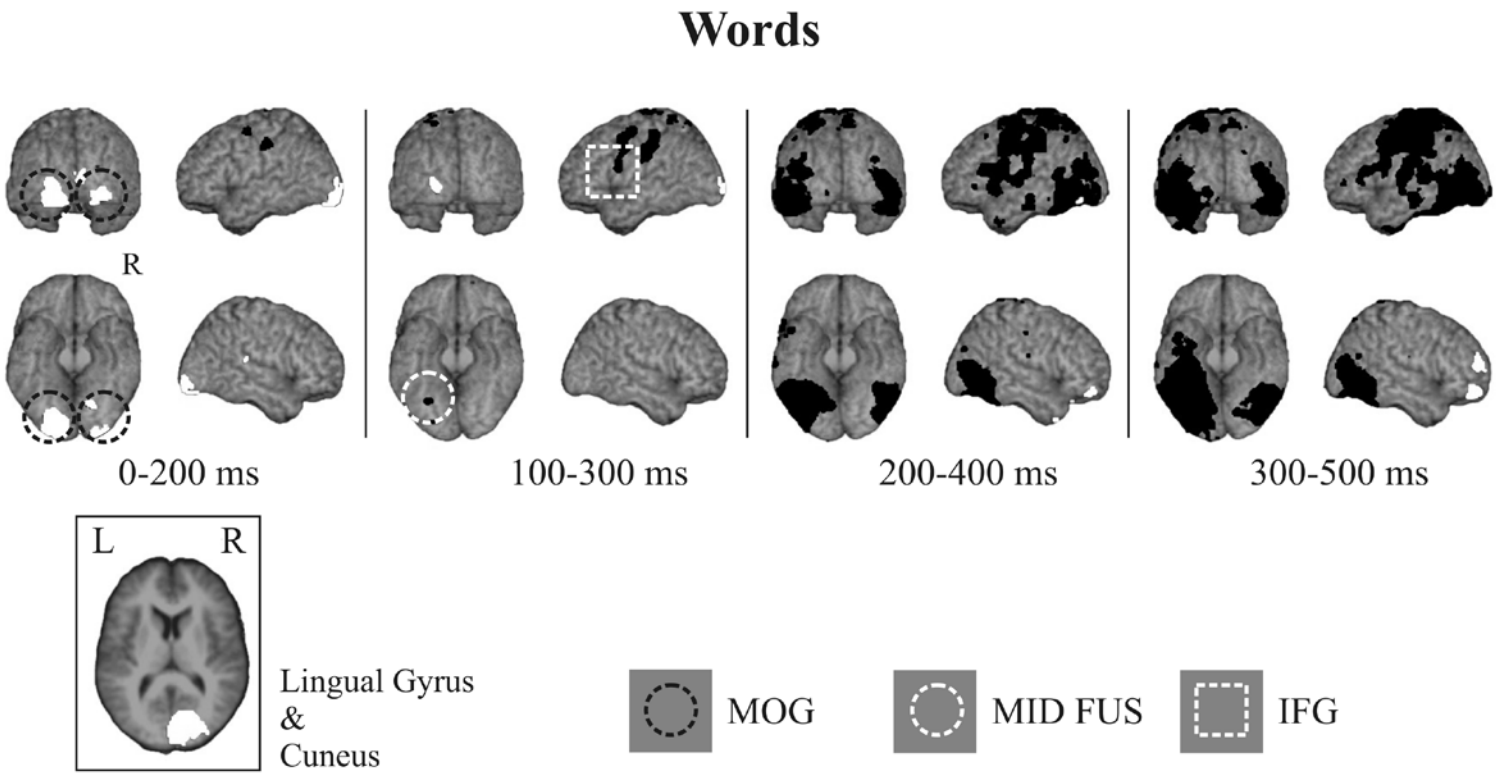

***Fig. 4 Group SAM maps of responses in the beta frequency band to centrally presented words. Left and right MOG activations appear as white ERS. Left and right fusiform gyus activations appear as black ERD***

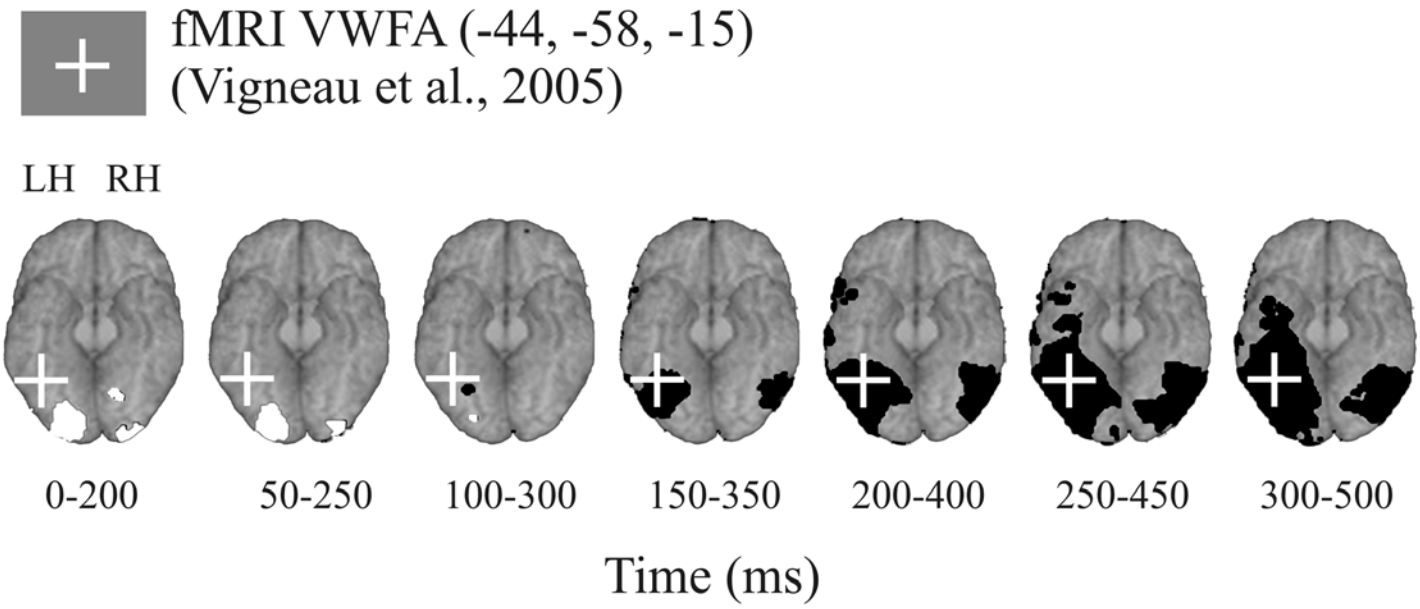

***Fig. 5 Group SAM maps of responses in the beta frequency band to 5-letter words presented to either the left or the right visual field. ERS and ERD thresholded at p<0.05 are shown in white and black respectively.***

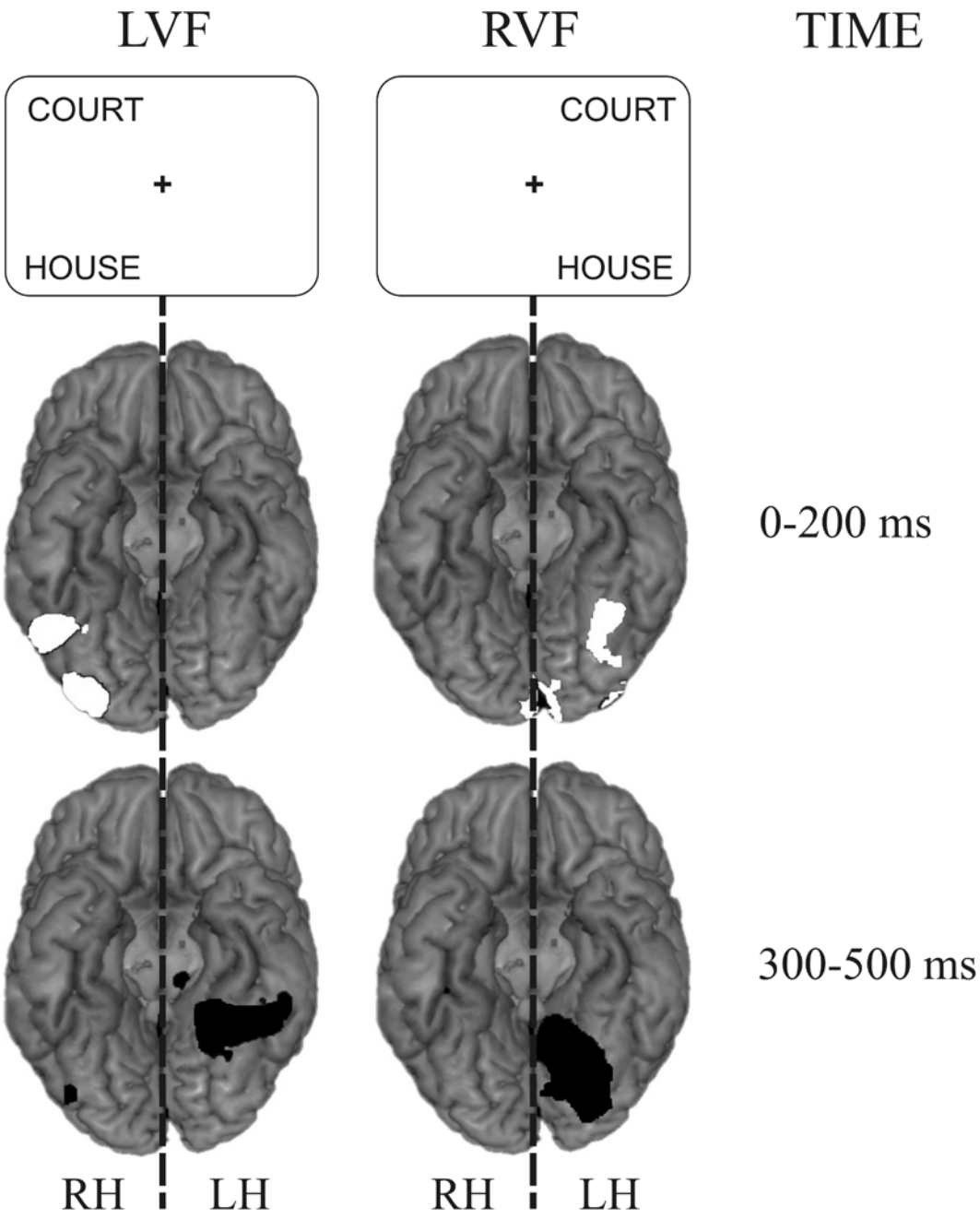

***Fig. 6 Phase synchronization and Granger causality estimates between left hemispere cortical network nodes during continuous reading. OT = inferior occipitotemporal cortex, MT = medial temporal cortex, ST = superior temporal cortex, AT = anterior part of the inferior temporal cortex, FM = face motor cortex, INS = insula, CB = cerebellum, PF = prefrontal cortex, ORB = orbital cortex.***

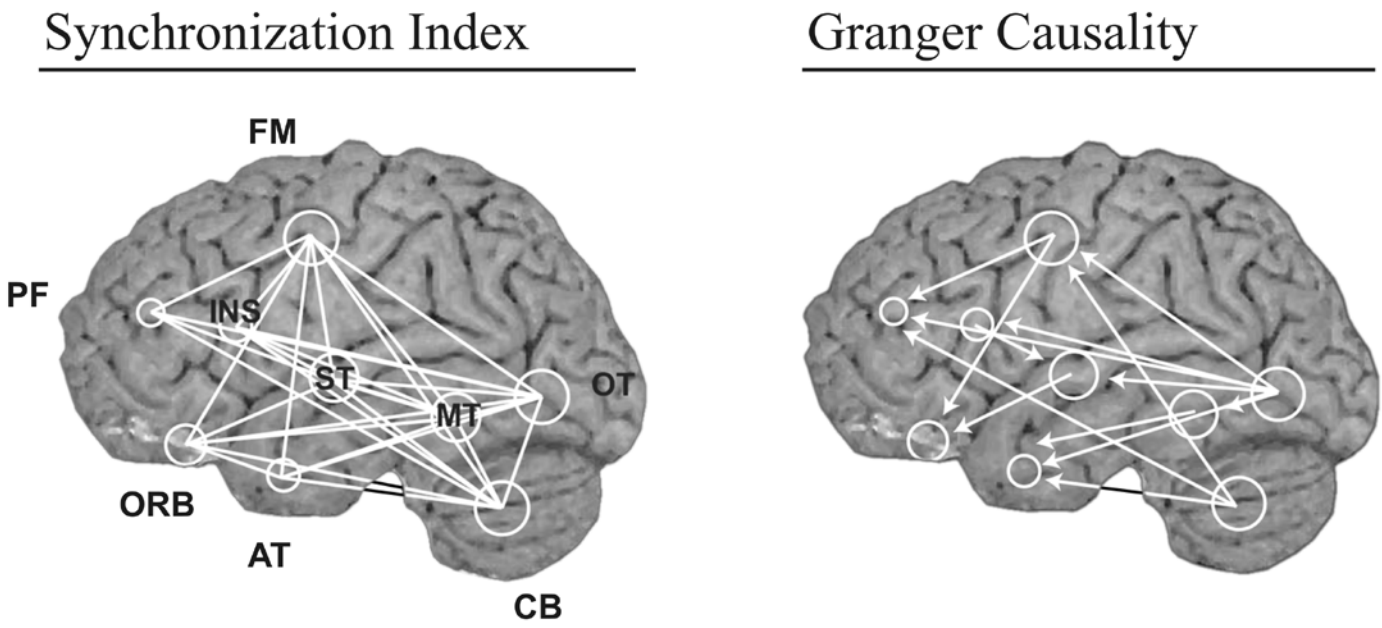

***Fig. 7 Shows: a) the normalised ERFs for centrally presented words in the left IFG (solid), compared with its right hemisphere homologue (dotted) as well as: b) word responses in the VWFA (solid) compared to its right hemisphere homologue (dotted). Black bars illustrate significant differences between each pair of time series (P <0.05) as computed with ROT-p.***

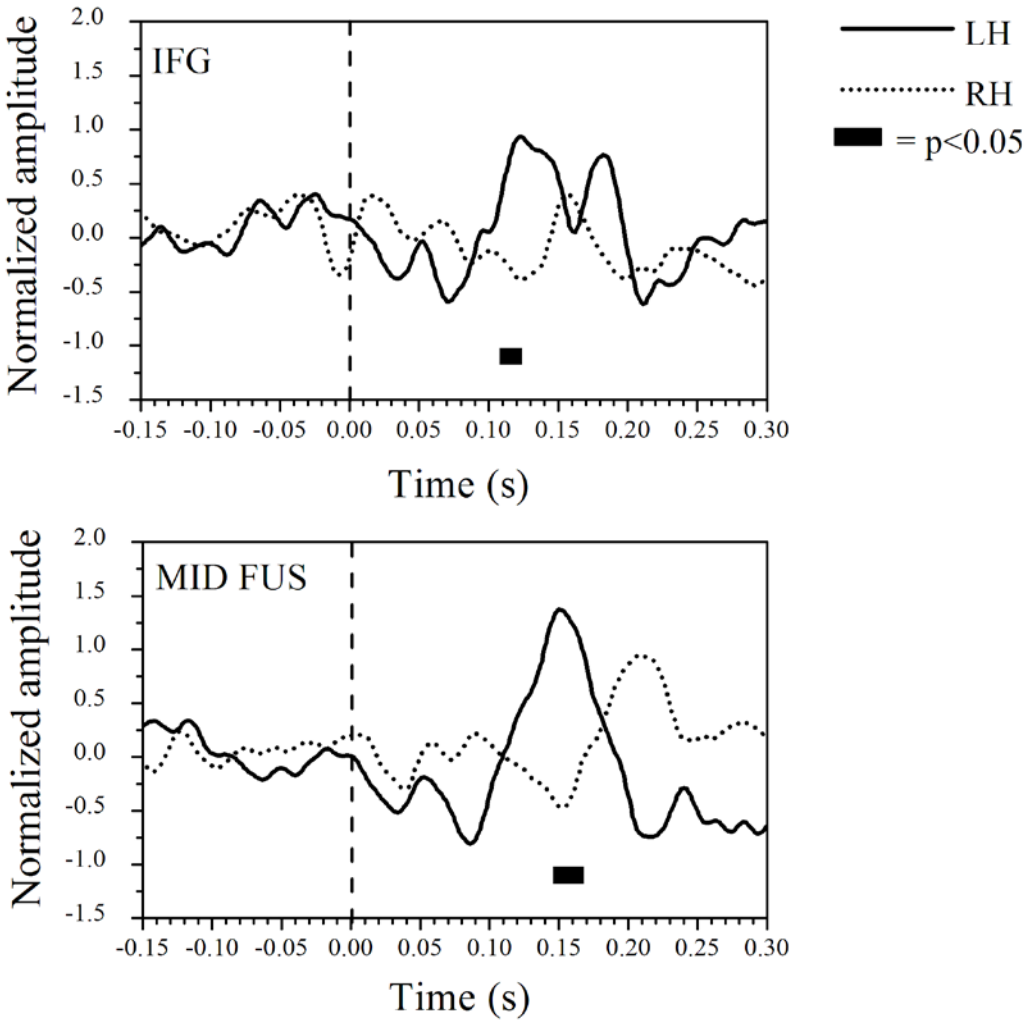

***Fig. 8 Shows: a) the normalised ERFs for centrally presented words (dotted) and faces (dotted), b) words (solid) and consonants (dotted) in all six virtual electrodes. Black bars illustrate significant differences between each pair of time series (P <0.05) as computed with ROT-p.***

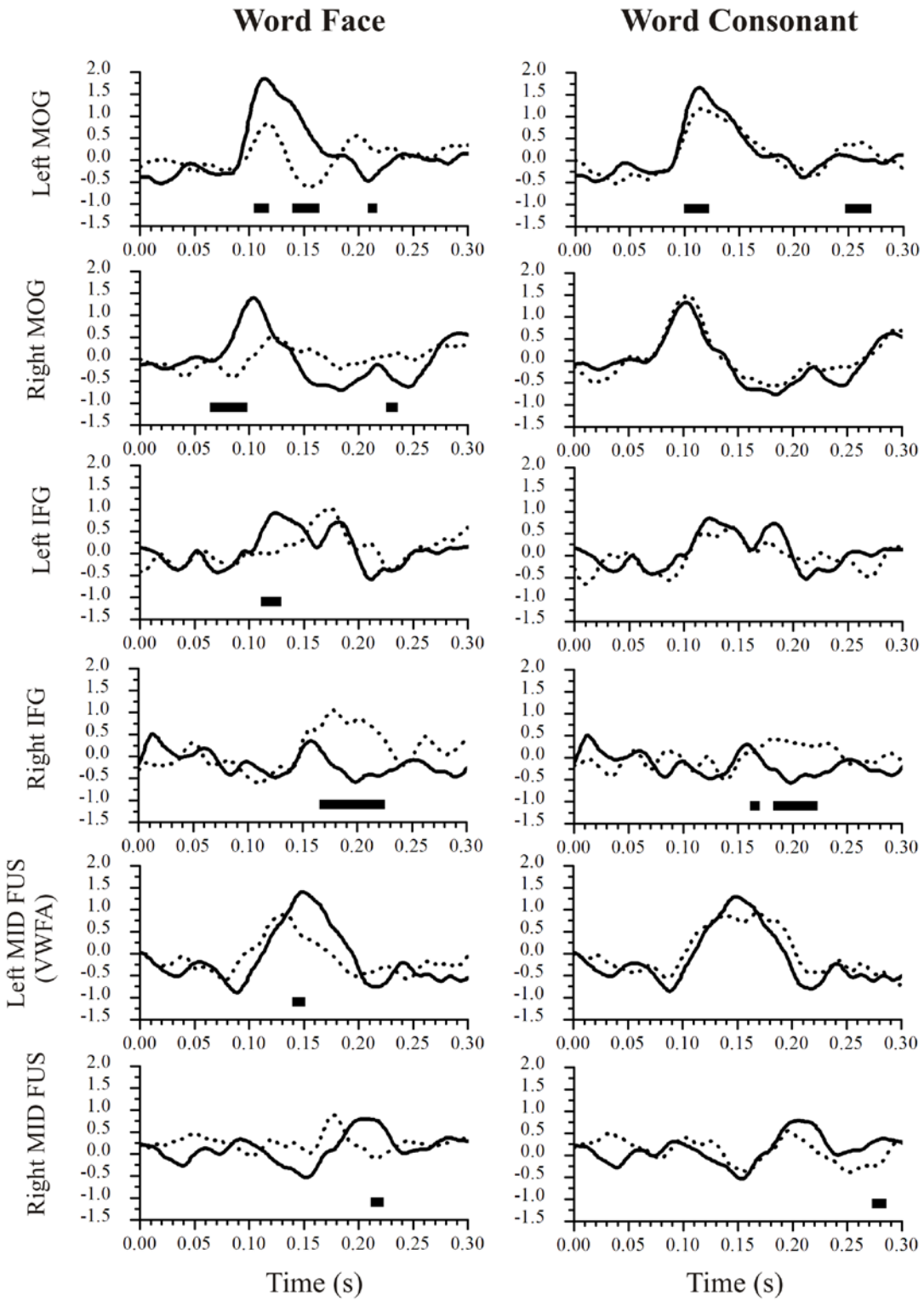

***Fig. 9 Shows the difference between time-frequency plots for words and consonant strings for the left IFG and left mid-fusiform ROIs. The black dotted lines represent regions in the time-frequency plots within which the difference between conditions reached significance at p<0.05, according to a general linear mixed model. To interpret the power scales, the values of x, and y for IFG(l) are 5 and 19 respectively. The values of x and y for MID-FUS(l) are 3.5 and18 respectively.***

***.***